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DISTRIBUTION OF FRESHWATER MUSSELS: COASTAL RIVERS AS BIOGEOGRAPHIC ISLANDS

J. JOHN SEPKOSKI, JR.* AND MICHAEL A. REX

Abstract

Sepkoski, J. J., Jr., and M. A. Rex (*Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 and Biology Department, University of Massachusetts—Boston, Boston, Massachusetts 02125*) 1974. *Distribution of freshwater mussels: coastal rivers as biogeographic islands*. *Syst. Zool.* 23:165–188.—Coastal rivers are isolated habitats that can be studied as biogeographic islands. Forty-nine rivers of the North American Atlantic and Eastern Gulf of Mexico Coastal Plains and their freshwater mussel (Unionidae) faunas are analyzed as a discrete island biogeographic system. Cluster analyses group the rivers on the basis of faunal similarity into five intergrading zoogeographic provinces. Distributional patterns in these provinces are strongly influenced by the proximity of species source rivers. Independent variables measuring stepping-stone distances (number of intervening rivers) from species source rivers, area of river drainage basins, and water quality parameters were tested in multiple regression models for their ability to predict numbers of species. Area of drainage basins is the best predictor of numbers of species. The species-area effect is greatest for provinces containing important source rivers and is lower for provinces in which rivers were colonized primarily by stepping-stone dispersal. The influence of stepping-stones on dispersal was assessed by constructing a stochastic model that uses immigration and extinction probabilities on serially arranged islands. Simulations of the model demonstrate that numbers of species on the islands should decrease approximately geometrically with distance from the species source. Numbers of freshwater mussels in the coastal rivers display a similar geometrical decline. The species-area and stepping-stone dispersal effects are combined in a descriptive model that stresses an interaction between area and distance from source rivers in determining species numbers. When combined with measures of environmental quality (hydronium concentration, amount of dissolved solids, and nitrate concentration), this model explains up to 80 percent of the variance in unionid species numbers among the coastal rivers. [Biogeography; freshwater mussels.]

MacArthur and Wilson (1963, 1967) developed their theory of equilibrial insular biogeography to explain, in part, variations in the numbers of species on oceanic islands. They did, however, note an analogy between true geographic islands and continental habitat islands, areas of relatively homogeneous ecology that are biogeographically isolated by dissimilar intervening areas. Although they did not pursue it, MacArthur and Wilson suggested that the same factors regulating numbers of species on oceanic islands should also be operating on habitat islands. The validity of their analogy has been recently demonstrated to varying degrees by Vuilleumier (1970) and Brown (1971) for mountaintop faunas and Culver (1970) and Vuilleumier (1973) for cave communities.

Another class of continental habitats amenable to insular biogeographic analysis is coastal river systems. Each river lies in its own basin, separated from its neighbors by open ocean at its mouth and drainage divides at the heads of its tributaries. These geomorphic boundaries effectively isolate the freshwater biota of each system.

The recent work of R. I. Johnson (1970, 1972, and unpubl.) on the systematics and distribution of freshwater mussels (Unionidae) presents the opportunity to study the insular biogeography of river systems. His faunal lists cover 79 species distributed among 49 rivers on the Atlantic and eastern Gulf of Mexico Coastal Plains of the United States, providing a large sample for statistical analysis. These data also offer a unique situation of a continental archipelago with nearly linearly arranged stepping stones spanning a wide latitudinal range. In this paper, we present an analysis of unionid

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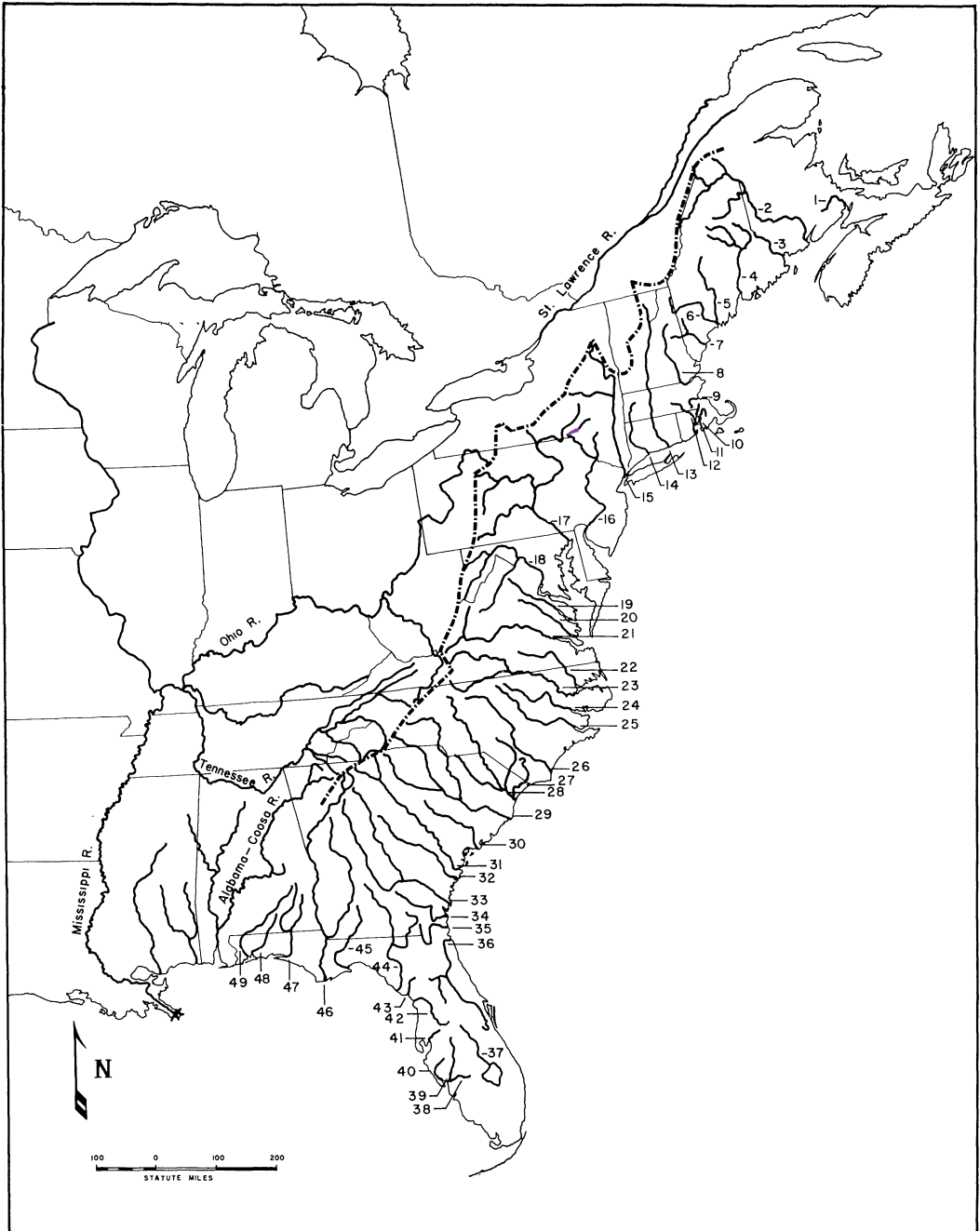


FIG. 1.—Map of the eastern United States, showing the river systems analyzed or referred to in the text. The heavy dashed line is the Appalachian Drainage Divide. Numbers on the map refer to the following rivers:

1. Petitcodiac,* 2. St. Johns, N.B.,* 3. St. Croix,* 4. Penobscot, 5. Kennebec, 6. Androscoggin, 7. Saco, 8. Merrimac, 9. Charles,* 10. Agawam,* 11. Blackstone, 12. Thames, 13. Connecticut, 14. Housatonic, 15. Hudson, 16. Delaware, 17. Susquehanna, 18. Potomac, 19. Rappahannock, 20. York, 21. James, 22.

species numbers based upon species-area relationships, distance effects, and environmental factors.

DISTRIBUTION OF FRESHWATER MUSSELS

The rivers of the Atlantic and eastern Gulf of Mexico Coastal Plains (Fig. 1) and their unionid faunas constitute a discrete biogeographic system. The Appalachian Divide borders the Atlantic Slope region to the west and the eastern Gulf Slope region to the north, effectively isolating the fauna of the coastal rivers from direct contact with the species-rich Interior Basin (Ortmann, 1913; Johnson, 1970). To the north the system is bounded by the St. Lawrence River and to the south by the Alabama-Coosa River System. Both of these rivers extend around the Appalachian Divide into the Interior Basin and are thought to have acted as dispersal routes into the coastal regions.

Figure 2 summarizes the distribution of the 79 species of freshwater mussels in 49 rivers along the Atlantic and eastern Gulf coasts. The figure displays a two-way cluster analysis of presence-absence data, performed using Jaccard's Coefficient of Association in the Q-mode (clustering of rivers) and Otsuka's Coefficient in the R-mode (clustering of species) (Cheetham and Hazel, 1969); clusters were formed in both cases by the unweighted pair-group method. The R-mode analysis is presented merely to order the species and not to define particularly interesting or "natural" groups. This dendrogram splits what appears to be a continuous transition from the Gulf faunas to the northern Atlantic faunas into an Atlantic group, a Gulf of Mexico and Florida group, and a group of endemics largely confined to the Gulf region.

The clustering of the rivers on the simi-

larities of their unionid faunas defines five faunal provinces:

1. Northern Atlantic Slope Rivers: characterized by a few (15) widely distributed species derived either from the Interior by route of the St. Lawrence River or from southern parts of the Atlantic Slope; includes all rivers from the Petitcodiac (New Brunswick) to Delaware.

2. Middle Atlantic Slope rivers: transitional between the Northern and Southern Atlantic regions, being characterized by 18 species of mixed northern and southern origin and two species not found elsewhere in the biogeographic system; includes rivers from the Susquehanna to Pamlico.

3. Southern Atlantic Slope rivers: characterized by a relatively diverse fauna of 33 species both endemic to the region and derived from the north or west (Gulf region); includes rivers from the Neuse to Altamaha.

4. Peninsular Florida rivers: characterized by a depauperate fauna of 14 species derived mostly from the west but including two endemics; includes rivers south of the Suwannee and Altamaha exclusively, with the very depauperate Waccasassa and Satilla Rivers best referable to this province.

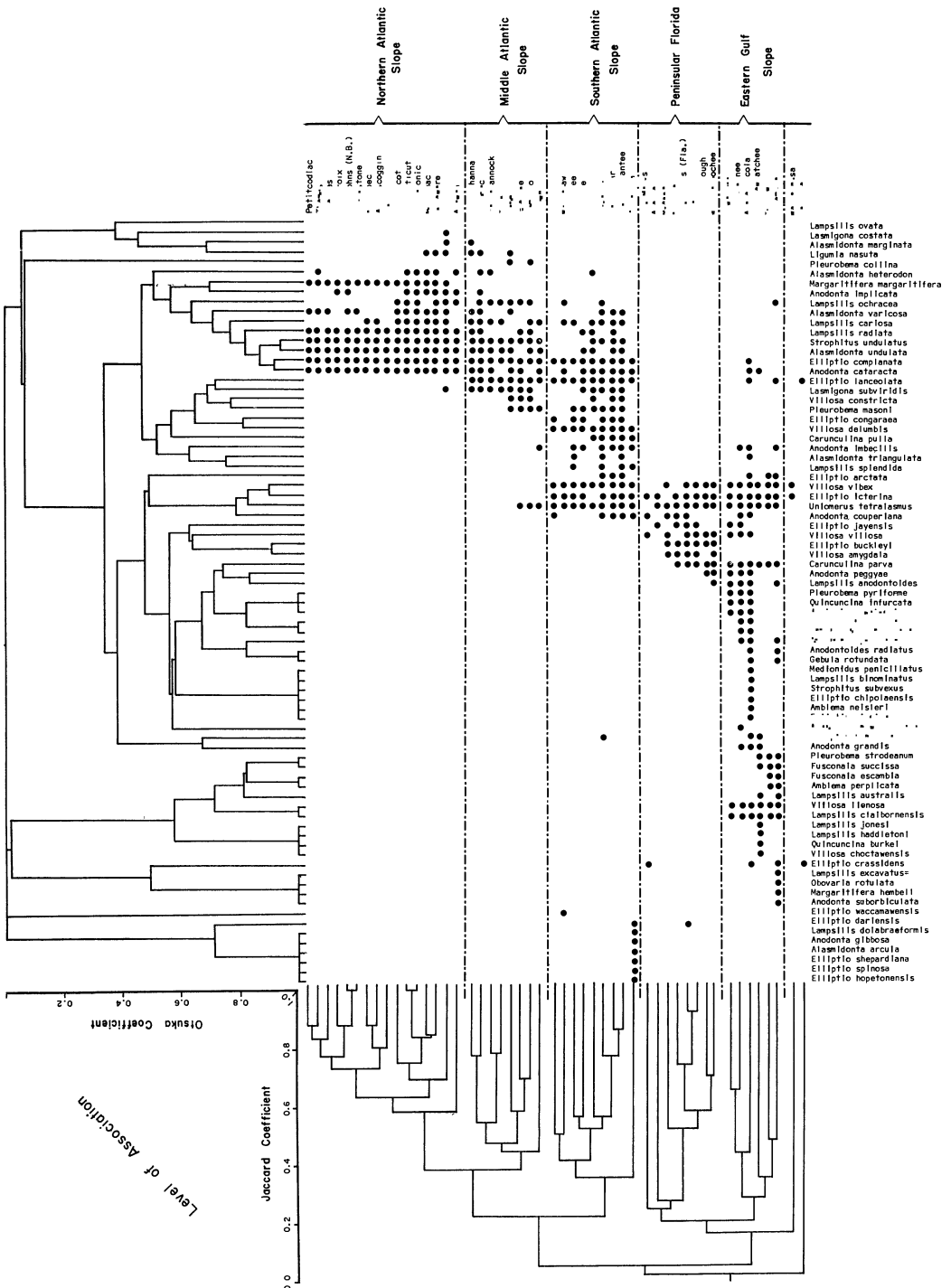
5. Eastern Gulf Slope rivers: characterized by a diverse fauna (49 species) of endemics and immigrants from the Interior via the Alabama-Coosa River System; four species of Southern Atlantic Slope origin are also present; includes rivers from the Suwannee to Escambia.

The above interpretations of source of origin for the species are taken from Johnson (1970).

We shall not extensively review previous explanations for this distributional pattern. Detailed discussions can be found in Ort-

←

Chowan, 23. Roanoke, 24. Pamlico, 25. Neuse, 26. Cape Fear, 27. Waccamaw, 28. Pee Dee, 29. Cooper-Santee, 30. Edisto, 31. Savannah, 32. Ogeechee, 33. Altamaha, 34. Satilla, 35. St. Marys, 36. St. Johns, Fla., 37. Kissimmee, 38. Alafia, 39. Peace, 40. Myakka, 41. Hillsborough, 42. Withlacoochee, 43. Waccasassa, 44. Suwannee, 45. Ochlockonee, 46. Apalachicola, 47. Choctawhatchee, 48. Yellow, 49. Escambia. Rivers not included in the regression analyses, because of unavailability of physical data, are marked (*).



mann (1913), van der Schalie (1945), Clench and Turner (1956), and Johnson (1970, 1972). However, a short synopsis of the methods and presuppositions of the classical zoogeographic approach is in order since several alternative hypotheses will be presented later.

The Unionidae are freshwater filter feeders that possess little vagility as adults. However, because of peculiar adaptations during their larval stages, unionids can rapidly disperse through an interconnected freshwater system. The glochidia (i.e., larvae) are parasitic and must select a suitable host fish in order to mature.¹ A glochidium attaches to a fish and encysts, usually in the gills, where it remains until it has assimilated the surrounding tissue (Lefevre and Curtis, 1912). It then metamorphoses and drops to the river or lake bottom as a young adult. The number of glochidia carried on a single host fish ranges from one to over 3,000 with an average of approximately 125 (Coker, et al., 1921).

Although some freshwater mussels appear to be taxon-specific in their selection of hosts (Coker, et al., 1921), little is known about the preferences of most species. But since unionids are largely intolerant of even brackish water (Cvancara, 1970), and because host selection occurs in freshwater, previous workers have assumed that all

mussels are inescapably confined to the river systems of their birth. Intersystem dispersion has been thought to be dependent solely upon geomorphic processes of stream capture (i.e., temporary confluence of tributaries) in headlands and coastal flooding at river mouths (van der Schalie, 1945). Ortmann (1913) and Johnson (1970, 1972) invoked specific Pleistocene and Holocene events to explain the pattern of unionid distribution throughout the coastal area of the eastern United States. As an example, the mixing of species in the Gulf and Southern Atlantic regions was thought to be a result of stream capture between the Apalachicola and Savannah Rivers. The presence in the Savannah of the restricted Gulf species *Elliptio fraterna* (Fig. 2) was cited as evidence of this route. Similarly, because of their restricted ranges, *Ligumia nasuta* and *Alasmidonta marginata* were believed to have entered the Atlantic Slope during the Pleistocene through the Mohawk and Susquehanna Rivers, respectively (Johnson, 1970). Once a foreign species entered a new region, its further dispersal was thought to be facilitated by coastal flooding during glacial low sea level stands.

This view of dispersion assumed that once a species colonizes a river it remains there unless eliminated by some major environmental event such as glaciation or marine transgression. In general, the ecological capacity of an individual river to support a suite of unionid species and the possibility of local extinctions through bio-

¹ The only known exceptions are *Strophitus undulatus*, *Anodonta imbecilis*, and possibly *Obliguaria reflexa*, all of which have some form of direct development (see Lefevre and Curtis, 1912; Howard, 1914).

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FIG. 2.—A two-way cluster analysis of the distribution of 79 species of freshwater mussels (horizontal axis) in 49 rivers (vertical axis) along the Atlantic and eastern Gulf of Mexico Coastal Plains. Dots indicate presence of a species. Jaccard's Coefficient of Association was used in the Q-mode (clustering of rivers) and Otsuka's Coefficient in the R-mode (clustering of species). Neither coefficient considers mutual absence of species (i.e., negative matches) in computing similarities; Green (1971) gives reasons for not considering mutual absence in ecological data analysis. Jaccard's Coefficient is influenced by sample size and leads to clusters of rivers that not only have similar species compositions but also similar numbers of species, an important consideration when defining faunal provinces. Q-mode cluster analyses employing other coefficients of association (i.e., Otsuka's, Fager's, and Simpson's, as defined by Cheetham and Hazel, 1969) display similar patterns of faunal provinces but place boundaries between provinces at slightly different locations, emphasizing the transitional nature of the boundaries and the high faunal similarity of the Florida and Gulf regions.

logical interactions were ignored. Such an approach breaks down when intraregional disjunct species are considered. Close faunal similarities of several well-separated rivers, such as the St. Johns (New Brunswick) and Blackstone, James and Pamlico, and Pee Dee and Ogeechee seem to indicate extinction in the intervening rivers. This, in turn, reduces the certainty that apparent dispersal routes are the true or only routes. Considering the complex geomorphic history of the southern Appalachian Mountains (Thompson, 1939; White, 1953; Hack, 1969), it is very possible that species of Interior origin introduced into the eastern Gulf region through the Alabama-Coosa River System may have reached the Southern Atlantic Slope by way of the Apalachicola to Savannah or Altamaha Rivers or directly from the Tennessee System through the Roanoke, Pee Dee, Santee, or Savannah Rivers.

Thus, the study of the distribution of freshwater mussels in terms of geomorphic phenomena provides only an incomplete understanding of processes of dispersal. Furthermore, it attempts to explain only why a particular species is found where it is and does not lend itself readily to analysis of faunal size. However, because unionids inhabit isolated drainage basins, questions as to why there are so many or so few species can be approached from insular biogeographic theory (MacArthur and Wilson, 1963, 1967). Through the construction of equilibrium models and their empirical solutions, theoretical explanations can be sought for both the observed distribution of species and the processes of dispersal.

APPROACH AND METHODOLOGY

Our primary interest in this analysis is to seek basic patterns among the rivers that influence the size of their unionid faunas. Thus, we are not interested so much in biological interactions as in the relationships between biological and physical (spatial, chemical, etc.) processes. Nor are we interested in the peculiarities of par-

ticular species or rivers but rather the common characteristics shared by all.

A useful technique for assessing relationships between biological and physical variables is stepwise multiple regression. This analytic tool has been widely employed in the analysis of species numbers of birds (Hamilton and Rubinoff, 1963; Vuilleumier, 1970; Power, 1972; and others), mammals (Brown, 1971), arthropods (Vuilleumier, 1973), and plants (Hamilton et al., 1963; Johnson et al., 1968; Johnson and Raven, 1973) on both oceanic archipelagos and continental habitat islands. Multiple regression is also useful as a method of fitting algebraic models to empirical data.

However, there are a number of statistical limitations in this type of least-squares analysis. Ecological data of the kind encountered in biogeographic studies are not ideally suited to multiple regression since the data rarely conform to multivariate normal distributions and independent variables are often highly intercorrelated. Moreover, regression analysis deals merely with correlations, which can often be entirely spurious; causation is always inferential. With these statistical shortcomings, we consider multiple regression only as a heuristic aid to understanding a biogeographic system. We use it to determine the relative importance of independent variables in predicting species numbers and to test the goodness of fit of various algebraic models.

Stepwise multiple regressions were performed using the BMDO2R computer program (Dixon, 1968). Iterative least-squares fits for nonlinear models were computed using a WANG 600-6 programmable desk calculator. Data used in our analyses are discussed in Appendix I.

RESULTS

Determinants of unionid species numbers

A series of stepwise multiple regressions were computed to assess the degree to which the independent variables discussed in Appendix I influence species numbers of freshwater mussels. We could make

TABLE 1. CORRELATION COEFFICIENTS BETWEEN ALL VARIABLES.¹

	Spp'	Spp	A	AC	AP	SL	SV	TM	TV
Spp'	—	—	—	-0.342	-0.304	0.209	-0.022	0.076	-0.119
Spp	—	—	0.646	-0.130	-0.118	0.098	-0.065	-0.067	0.172
A	—	0.552	—	0.196	0.171	-0.093	-0.075	-0.191	0.396
AC	-0.395	-0.253	0.133	— *	0.947*	-0.813*	0.253*	-0.742*	0.639*
AP	-0.379	-0.235	0.140	0.994*	— *	-0.807*	0.273*	-0.771*	0.679*
SL	0.344	0.256	-0.054	-0.985*	-0.972*	— *	-0.579*	0.892*	-0.649*
SV	-0.133	-0.126	-0.027	0.663*	0.674*	-0.654*	— *	-0.570*	0.443*
TM	0.138	0.033	-0.147	-0.885*	-0.893*	0.875*	-0.726*	— *	-0.792*
TV	-0.221	-0.012	0.298	0.828*	0.834*	-0.794*	0.616*	-0.835*	— *
NO ₃	-0.142	-0.053	0.117	0.378	0.363	-0.353	0.232	-0.292	0.468
Ca	-0.271	-0.227	-0.003	-0.267	-0.293	0.304	-0.126	0.441	-0.270
H-C	-0.304	-0.259	-0.010	-0.262	-0.290	0.300	-0.138	0.439	-0.258
H-N	-0.326	-0.284	-0.023	-0.163	-0.183	0.189	-0.102	0.340	-0.206
DS	-0.303	-0.329	-0.142	-0.270	-0.300	0.285	-0.157	0.438	-0.319
Cl	-0.183	-0.183	-0.056	-0.214	-0.233	0.208	-0.138	0.338	-0.251
HCO ₃	-0.057	-0.040	0.014	-0.264	-0.286	0.291	-0.129	0.310	-0.200
pH	0.078	0.133	0.110	-0.250	-0.255	0.283	-0.116	0.119	-0.203
H	-0.238	-0.305	-0.199	0.026	0.014	-0.047	-0.057	-0.062	-0.006
	NO ₃	Ca	H-C	H-N	DS	Cl	HCO ₃	H	pH
Spp'	-0.022	-0.002	-0.056	-0.341	-0.101	-0.189	0.206	0.230	-0.203
Spp	0.043	-0.069	-0.200	-0.392	-0.251	-0.250	0.275	0.213	-0.199
A	0.093	-0.105	-0.119	-0.213	-0.273	0.166	0.186	0.059	-0.068
AC	0.510	-0.202	-0.188	0.155	-0.125	-0.118	-0.211	-0.203	0.213
AP	0.429	-0.258	-0.251	0.199	-0.196	-0.163	-0.247	-0.247	0.259
SL	-0.316	0.300	0.085	0.317	0.270	0.295	0.302	0.271	-0.285
SV	0.333	0.117	0.322	-0.056	0.051	-0.122	0.148	0.026	-0.019
TM	-0.303	0.379	0.405	0.111	0.400	0.417	0.253	0.296	-0.301
TV	0.398	-0.337	-0.336	-0.086	-0.347	-0.218	-0.206	-0.284	0.289
NO ₃	—	0.255	0.264	0.443	0.334	0.242	0.013	0.028	-0.003
Ca	0.058	— *	0.990*	0.684*	0.893*	0.494*	0.592	0.660	-0.656
H-C	0.056	0.987*	— *	0.702*	0.919*	0.541*	0.589	0.659	-0.656
H-N	0.103	0.835*	0.867*	— *	0.724*	0.606*	0.069	0.290	-0.287
DS	0.081	0.895*	0.936*	0.862*	— *	0.715*	0.433	0.550	-0.537
Cl	0.241	0.525*	0.584*	0.541*	0.683*	— *	0.137	0.223	-0.225
HCO ₃	-0.070	0.560	0.542	0.067	0.446	0.240	— *	0.789*	-0.787*
pH	-0.155	0.506	0.490	0.125	0.418	0.241	0.765*	— *	-0.996*
H	0.148	-0.286	-0.275	-0.106	-0.199	-0.116	-0.358*	-0.777*	— *

¹ Coefficients in the upper triangle were obtained by using log transformed data and those in the lower triangle by using untransformed data. Spp' indicates partial correlations with species numbers with the effect of area removed. Spp represents simple correlations with species numbers. All other symbols are explained in the text. Correlations which are significant at the 5 percent level are italicized and those significant at the one percent level are in boldface italics. The three major groups of redundant independent variables discussed in the text are marked with asterisks.

causal inferences only after a number of different regression analyses had been performed. Below we present only our major findings on the relationships between numbers of unionid species and habitat area, dispersal distances, and parameters of environmental quality. A more detailed documentation of our regression analyses is provided in Appendix II.

Environmental quality

The relationship of each measure of environmental quality to species numbers is difficult to interpret because of high inter-correlations among many of them (see Table 1). This high statistical redundancy led to erratic results when all independent variables were regressed together against number of species. Often, for instance,

several related measures of environmental quality entered the multiple regressions with different uninterpretable signs (see Appendix II, 1, 2). Most of the redundant variables were therefore eliminated from later analyses, a procedure recommended by Snedecor and Cochran (1967).

As Table 1 indicates, some of the highest correlations occur among variables describing water hardness: calcium concentration, carbonate hardness, non-carbonate hardness, and dissolved solids. Chloride concentration is also redundant with this group, primarily because Florida rivers, flowing over low limestone terrain, tend to be both very hard and relatively saline. All five variables are negatively correlated with species number, several becoming marginally significant when area is partialled out (Table 1). These correlations result more from peculiarities of Florida rivers than from any overall trends in the coastal biogeographic system. The depauperate unionid faunas of peninsular Florida may be related to high concentrations of dissolved minerals or to environmental instability caused by hurricane-induced salt water incursions, which average chloride concentrations measure only indirectly. Or, the correlations of water hardness and chloride concentration with species number may be spurious; low numbers of species in Florida may be due instead to the relatively small habitable areas afforded by the poorly developed drainage systems. The general increase in correlations between species number and measures of water hardness when area is partialled out support the latter hypothesis. However, our analysis could not resolve this ambiguity. Dissolved solids was retained from this group of variables in later regressions since it has the highest simple correlation with species number and generally entered the multiple regressions at a higher level of significance than other measures of water hardness.

A second group of redundant measures of environmental quality are those related to acidity: pH, hydronium concentration,

and bicarbonate concentration. These variables are also significantly correlated with some measures of water hardness, reflecting the role of CaCO_3 in buffering pH. Of the three acidity variables, hydronium concentration is the only significant predictor of species numbers. Statistically, it accounts for the low number of species in the unusually acid Satilla and St. Marys Rivers. Johnson (1970) suggested that the association between low number of species and high acidity in these two rivers was causal.

A third group of statistically redundant variables includes annual temperature mean and variance and measures of dispersal distance. These correlations result from the location of the inferred species-source rivers in the north and south. Both temperature and dispersal distances correlate with a south to north decline in species numbers. When effects of dispersal distances are partialled out in multiple regression, the correlation between species number and mean temperature becomes negative (Appendix II, 5); this is due to the proximity of the warm but depauperate Florida rivers to the southern end of the biogeographic system. Since this spurious result could lead to obviously incorrect conclusions, temperature variables were excluded from later regression analyses. The relevance of temperature to number of unionid species is considered in later discussion.

Nitrate concentration also shows weak but significant correlations with temperature and dispersal variables (Table 1). These result from the unusually high nitrate concentrations in several northern rivers. Nitrate was retained throughout our multiple regression analyses since it displayed a persistent, if only marginally significant, positive relationship with species number.

As a whole, the environmental quality variables explain a relatively small part of the variance in number of unionid species, about 31 percent in the case of linear multiple regression and 46 percent in a model using log-transformed data (Appendix II, 1). When regressed with area and dispersal distances, variables measuring environ-

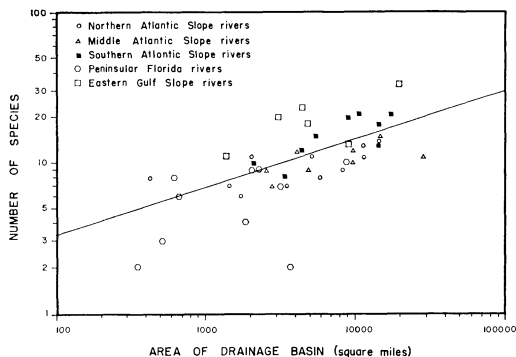


FIG. 3.—A double-logarithmic scatter plot of unionid species number versus area of drainage basin. The curve is a plot of text Equation 2. The rivers are divided by symbols into 5 groups identical to those defined by the Q-mode cluster analysis (Fig. 2).

mental quality assume a predictive role subordinate to the biogeographic parameters and explain only 10 to 20 percent of the variance in species numbers. These low correlations may be due in part to pollution of many coastal rivers subsequent to the sampling of their faunas (collections studied by Johnson dated from mid-19th century to the present). However, the high predictive value of the biogeographic variables alone ($R^2 > 0.60$) leads us to believe that the subordinate predictive role of the variables measuring environmental quality is real.

Area

The relationship between number of species (S) and area of islands (A) is well known (see reviews in MacArthur and Wilson, 1967; Johnson and Raven, 1970; and Simberloff, 1972) and can generally be expressed as

$$S = CA^z \quad (1)$$

where C and z are fitted constants. Preston (1962) derived a value of 0.26 for z , which he proposed as a theoretical constant. However, analysis of a number of different ecological situations has demonstrated that z varies over a range of approximately 0.2 to 0.4 (Hamilton et al., 1964; MacArthur and Wilson, 1967; Johnson and Raven, 1970).

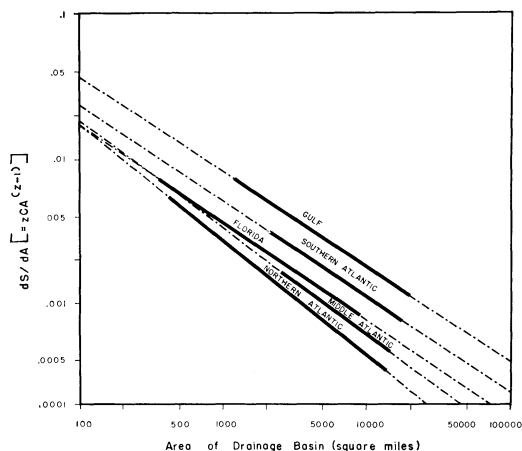


FIG. 4.—A double-logarithmic plot of first derivatives of the species-area curve (text Equation 1) against area of drainage basin for five groups of rivers as defined in Table 2. The solid portion of the lines indicates the range for which there is data control; dashes extend the lines without control to the margins of the graph.

MacArthur and Wilson (1963, 1967) theorized that the change in number of species with change in area (i.e., dS/dA) is not dependent solely upon area but is also a function of rate of immigration and size of the species pool. This relationship has been interpreted by some (e.g., Brown, 1971) to mean that z varies monotonically with dS/dA . But this is not necessarily true since differences in both C and z affect dS/dA . It is possible, in fact, for two groups of islands with similar faunas to display values of dS/dA that are larger for the first group over small islands and greater for the second group over larger islands if $C_1 > C_2$ and $z_1 < z_2$. Furthermore, in statistical analysis, C and z are interdependent (see Footnote 2, equation 1' below), and analytic methods that tend to reduce the estimate of z will increase the estimate of C and vice versa. Such analysis is further complicated in multiple regression since other independent variables regressed in league with area alter the estimates of C and z considerably (Hamilton et al., 1964; our Appendix II, 2, 3, 4).

Area is the single best predictor of unionid species number in the biogeographic system being considered (Fig 3). The relationship between number of species and area is best described by the curve²

$$S = 0.780A^{0.316} \quad (2)$$

which has a correlation coefficient of 0.602 ($P < .001$). It should be remembered that these C and z values are not directly comparable to other studies, since area in this case is a nonlinear estimate of actual habitable area (Appendix I).

Interesting variations in C and z occur if species-area curves are computed for subsets of the 44 rivers. Table 2 gives iterative solutions of equation 1 for five groups of rivers similar to the faunal provinces defined by the Q-mode cluster analysis. First derivatives of these curves are displayed graphically in Figure 4. The relative

² There are several ways to fit the species-area curve (text equation 1) to a set of data. We employed an iterative least-squares technique, using successively better estimates of z and solving the equation

$$\frac{1}{n} \cdot \sum_{i=1}^n \frac{S_i}{A_i^z} = C \quad (1')$$

The best estimate of z is that which minimizes the quantity

$$\sum_{i=1}^n (S_i - CA_i^z)^2 \quad (2')$$

We feel that for descriptive purposes, this method is superior to the regression model

$$\log S = \log C + z \log A \quad (3')$$

Although equation (3') is mathematically identical to text equation (1), it is not statistically identical (Zar 1968) since its least-squares solution minimizes

$$\sum_{i=1}^n [\log S_i - \log (CA_i^z)]^2 \quad (4')$$

This has the effect of giving differential weight to, and therefore producing better fits for, those data points close to the origin, i.e., those cases with small S_i and A_i (Glass 1969). The iterative method weights all data pairs equally and has constant descriptive value regardless of proximity to the origin.

TABLE 2. ESTIMATED PARAMETERS OF SPECIES-AREA CURVES (TEXT EQUATION 1).¹

Faunal province	Number of rivers	C	z	Correlation
Northern Atlantic	11	1.92	0.193	0.679
Middle Atlantic	7	1.11	0.258	0.764
Southern Atlantic	9	0.728	0.339	0.757
Peninsular Florida	9	0.681	0.311	0.850
Eastern Gulf	5	1.12	0.342	0.942

¹ For five groups of rivers similar to those defined in the Q-mode cluster analysis of rivers by their unionid faunas (Fig. 2). The following are the differences: the relatively acid Satilla and St. Marys Rivers fall far below the species-area curve for the other Florida rivers and were therefore not included in computations; the Susquehanna River, in its isolated position at the head of Chesapeake Bay, falls far below the curve for the Middle Atlantic rivers and was not included in computations; the Suwannee River falls far below the curve for the Gulf rivers but on the curve for the adjacent Florida rivers and was therefore included with the latter in computations. Estimators were computed using the iterative method outlined in Footnote 2.

heights of the lines (dS/dA vs. A) in the double logarithmic graph indicate the degree to which species number varies differentially with area in the five regions. The Gulf and Southern Atlantic provinces display the largest dS/dA , presumably because both regions include species source rivers. The larger species pools in the Alabama-Coosa and Apalachicola Rivers probably explains the higher differential of the Gulf province.

Simple distance from the source rivers cannot explain the lower magnitudes of dS/dA for the Florida, Middle Atlantic, and Northern Atlantic rivers since biogeographic theory predicts that the effects of area should increase with distance. A better hypothesis is that dispersal of freshwater mussels over large distances is dependent upon intermediate stepping stones. If each river acts as the major source area for the river next more distant from the primary source, one would expect to observe a continual decline in dS/dA when following a string of stepping stones away from an initial source (MacArthur and Wilson, 1967). The low differential for the Northern Atlantic rivers would thus appear to indicate that few immigrants arrive from the St. Lawrence River, one of our hypothesized source rivers. This problem will be discussed at greater length in later sections.

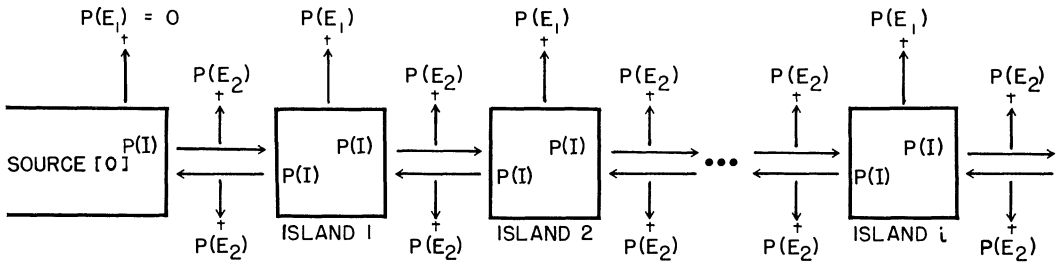


FIG. 5.—A graphical representation of the model developed to simulate immigration and extinction along a linear array of stepping-stone islands. The squares represent equally sized and spaced islands. The open rectangle to the left is the species-source area, upon which species never become extinct. During any interval of time, each species on any island has an equal positive probability $P(E_1)$ of extinction, represented by the vertical arrows and crosses extending upward from the islands. Each species on an island also has an equal probability $P(I)$ of dispersing propagules to the two neighboring islands; dispersion is represented by horizontal arrows. Propagules have a probability $P(E_2)$ of extinction before successful colonization, represented by arrows and crosses extending vertically from the dispersal arrows.

Distance effects

The bivariate analysis of species numbers and area demonstrates a strong correlation and presumably causal relationship. However, this causation largely involves extinction, with increase in area decreasing probabilities of extinction (Diamond, 1969, 1973; Simberloff, 1972). Any consideration of equilibrial insular biogeography as developed by MacArthur and Wilson (1963, 1967) must also include analysis of the effects of immigration. The inclusion of dispersal distances along with area and selected measures of environmental quality in the multiple regression analyses greatly increased the proportion of variance in species numbers explained by the equations (Appendix II). However, it is not immediately clear what algebraic form the models should take in order to be ecologically meaningful; several linear and non-linear equations were tested.

We acquired some insight into this problem by constructing an independent stochastic model based on the processes of immigration along stepping stones. This model abstracts from the real biogeographic system several factors known or thought to be important in influencing numbers of species. Its accuracy can be assessed by determining the extent to which it simulates

the actual biological situation as reflected in the available data.

In order to keep the analysis simple, all species were considered to have identical biogeographical properties (i.e., immigration and extinction rates) and all islands to be of equal size and distance apart. These assumptions make per species immigration and extinction rates independent of any particular island. In order to approach the spatial arrangement of coastal river systems, the islands in the model were given a linear configuration. A species source, defined as an "island" upon which no species ever becomes extinct, was placed at one end of the linear array. Thus, the model was constructed such that the islands can behave as stepping stones leading away from the source area.

Given these entities, we postulated several possible events during any given interval of time (Fig. 5). If a species inhabits any island i , it can either (1) continue inhabiting i , or (2) it can become extinct on i . The species population on i can also disperse propagules capable of colonizing neighboring islands. Unionids are probably poor dispersers since they can survive only short periods in the environments between isolated freshwater systems. Therefore, it is reasonable to assume in the model that the

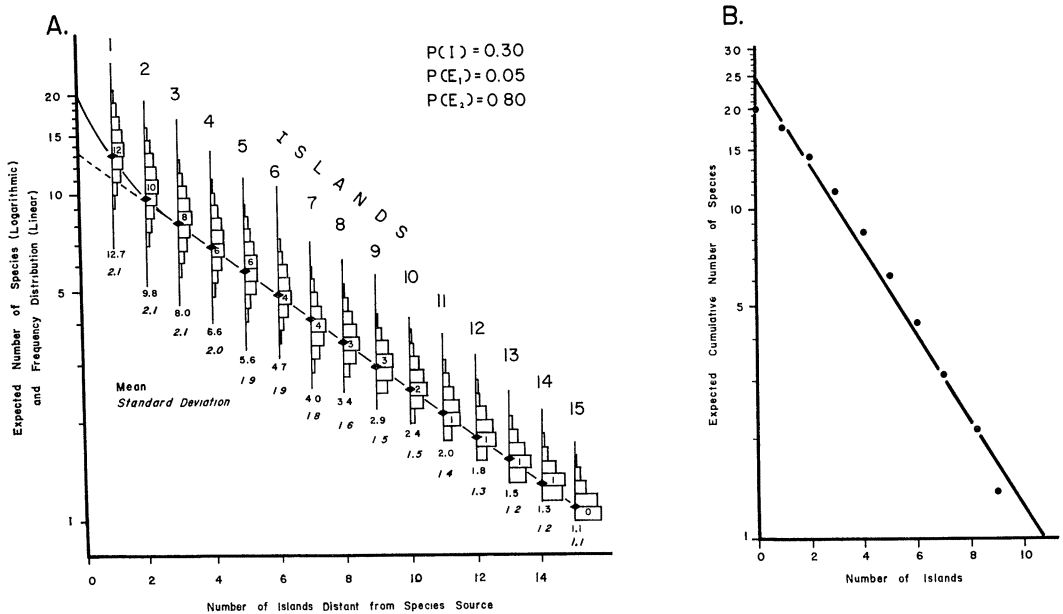


FIG. 6.—Graphical display of the results of a simulation of immigration and extinction along a linear array of stepping-stone islands. The probability of extinction of an established population $P(E_1)$ is 0.05; the probability of emigration to a neighboring island $P(I)$ is 0.3; and the probability of emigrants becoming immediately extinct $P(E_2)$ is 0.8. A. Semilogarithmic graph of numbers of species on the islands when the source area (Island 0) has an invariant species number of 20. The expected (mean) number of species (solid diamond) is plotted logarithmically against a linear axis representing the variation in species numbers that can occur at equilibrium; only the modal frequencies are numbered. Note that beyond Island 1 the expected numbers of species can be adequately described by a geometric series (straight line). B. Semilogarithmic cumulative graph of the average number of islands that each species inhabits. This distribution can also be approximated by a geometric series (straight line).

probability of immigration to an island two or more steps from the point of emigration is insignificant relative to the probability of reaching the nearest island (see MacArthur and Wilson, 1967:123 ff.). So, for a species on i , two more events are possible: (3) it can send forth propagules to invade the next island more distant from the primary source ($i + 1$), and (4) it can emit propagules to invade the next island less distant ($i - 1$). We assumed that only events (1) and (2) were mutually exclusive during any single interval of time and that any other combination of one, two, or three events was possible.

Given these discrete entities and events, specific probabilities could be assigned to

each event and the modeled system could be solved to determine what, if any, equilibrium configuration of species numbers occurs over the islands. Although we could not solve this model analytically, we did run a number of Monte Carlo computer simulations.³ Figure 6a is a graphical representation of one simulation, using a pool of 20 species on the source island. Several patterns are immediately obvious from the graph. First, the probability of any single species being on an island decreases geometrically away from the source, except on

³ Further documentation of the algorithm employed in the computer simulations is available upon request from Sepkoski.

those islands closest to the source. This relationship can be expressed as

$$P_i(S_j) \propto X^i \quad (3)$$

where

$P_i(S_j)$ = probability of the j^{th} species being on the i^{th} island,

i = number of stepping stones (islands) distant from the source, where i is greater than approximately 2 or 3,

X = base of the geometric series, with $0 < X < 1$.

The base of the geometric series X increases with increasing probability of immigration and decreasing probabilities of extinction. If the rigid stipulation that a species cannot become extinct on the source is replaced by a positive but very small probability of extinction, the geometric series will better describe the islands close to the source. However, if the system is finite, it then has only a quasi-equilibrium and all species will eventually become extinct.

The expected number of species beyond the second or third stepping stone is approximated by

$$E(S_i) = (P/k)X^i \quad (4)$$

where

$E(S_i)$ = expected number of species on the i^{th} island,

P = size of the species pool,

k = constant, generally with $1 < k < 2$.

However, there is a high variation about the expected number of species and the frequency distributions are generally platykurtic (Fig. 6a). If this is true of real biogeographic systems, then the observed number of species on any island can be only a rough estimate of the expected number.

Another pattern that was monitored during the simulations is the average number of islands upon which each species occurs. Figure 6b is a plot of the cumulative distribution of islands per species. Note again that this distribution can be roughly approximated by a geometric series, although there are systematic deviations.

These observations from the simulations

compare favorably with actual data. Figure 7 is a set of four graphs in which the logarithm of the number of species shared with a given source river is plotted against number of rivers distant from that source. All plots display some tendency toward a geometric decline in the number of shared species per river as the source becomes more distant. Much of the scatter is due to variation in area and environmental quality and possibly to the inherently stochastic variation implied by the simulations. If Florida rivers, with their generally small areas and harsh environments, are eliminated from analysis, geometric series can be fit to all graphs with highly significant correlations ($P < 0.01$). Notice that in all cases except the St. Lawrence there is a definite tendency for deviations above the curve to increase near to the source river.

The actual cumulative distribution of islands per species for all 44 rivers and 79 species (Fig. 8) is strikingly geometric ($r > 0.98$). There are fewer widely distributed species than the fitted curve suggests, a pattern similar to that in the simulated models. However, there are more sparsely distributed species than the model would predict. This may result from a relatively large number of endemic unionid species (24 species or 30% of the total fauna) not shared with the source rivers.

From these similarities between patterns of species distributions predicted by the stochastic model and observed in the data we conclude that the modeled stepping-stone processes of immigration explain to a large extent the effects of distance observed among unionid species numbers in our biogeographic system. It is interesting to note that, in a study of the avifauna of the southwest Pacific islands, Diamond (1972, 1973) also observed a geometric decline in species numbers over large distances from New Guinea. We concur with Diamond's suggestion that stepping-stone islands play an important role in immigration throughout this region.

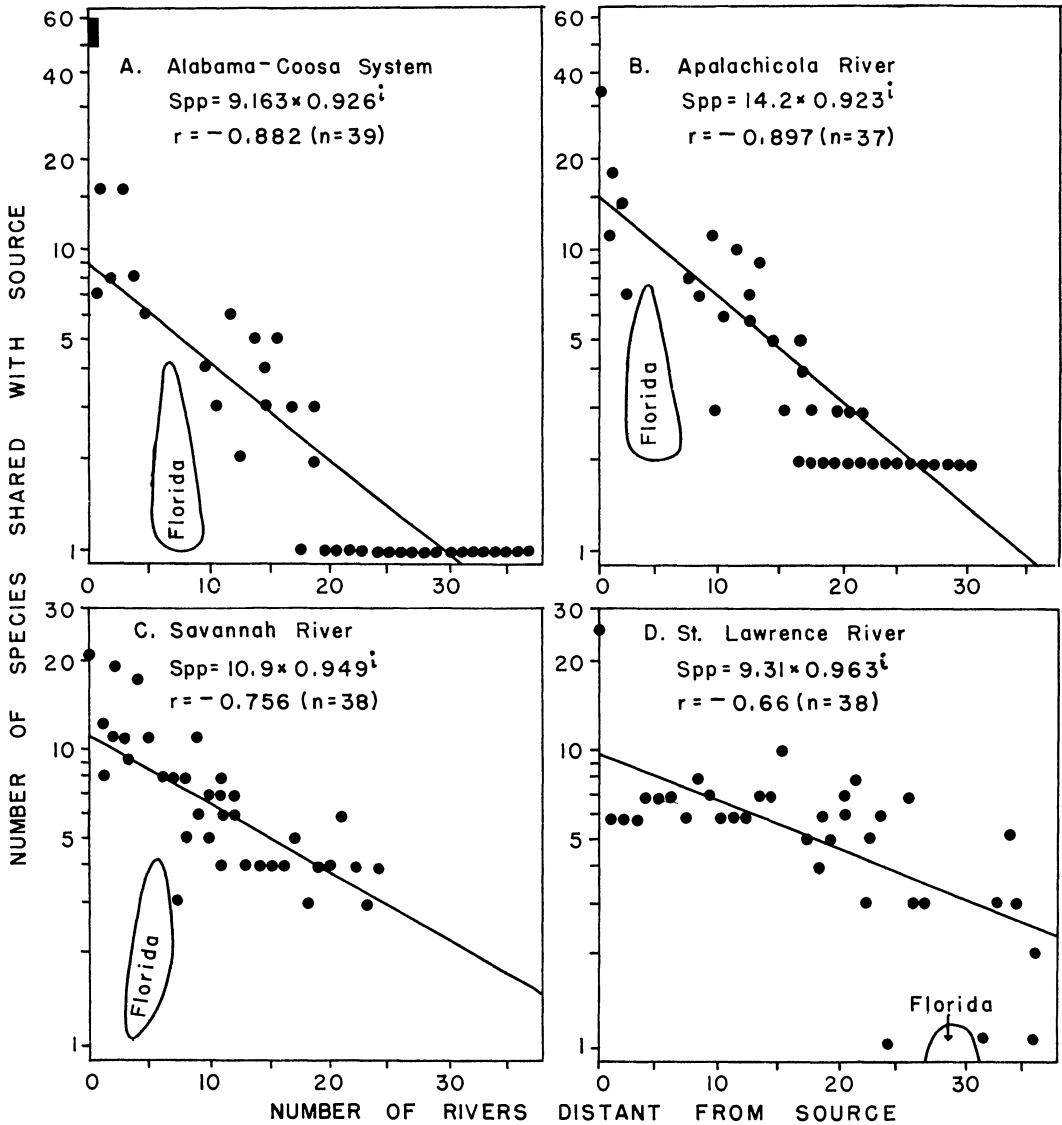


FIG. 7.—Semilogarithmic plots of the number of species shared with each of the four hypothesized species source rivers. Compare these graphs to Figure 6a. In all cases, a geometric series (straight lines for which equations are given) can be fitted to the data with highly significant ($P < 0.001$) correlations (r). The encircled areas include all rivers of peninsular Florida; these were not included in computations. Regressions were computed by transforming shared number of species to logarithms.

Quantitative description

The results of the previous analyses can be briefly summarized as follows:

1. Estimated habitable area appears to influence unionid species numbers more than any other single variable, alone ex-

plaining 36 percent of the variance in numbers of species; this influence decreases with increasing distance from the species source rivers.

2. Species numbers decline geometrically as stepping-stone distances from the source rivers are increased.

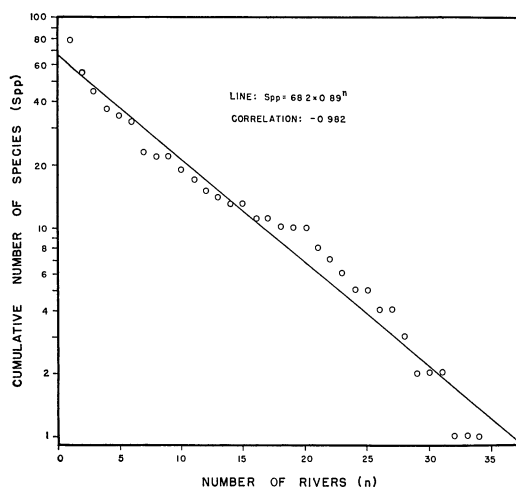


FIG. 8.—Semilogarithmic plot of the cumulative distribution of number of rivers in which each species occurs, read as 79 species inhabit at least one river, 55 inhabit at least two, etc. Compare this graph to Figure 6b. The straight line is the regressed geometric series describing this distribution. This regression was computed by transforming the cumulative number of species to logarithms.

3. Variation in the environmental quality of the generally benign rivers accounts for a subordinate amount of variance in species numbers; the most influential variables appear to be hydronium concentration, amount of dissolved solids, and nitrate concentration, together correlating mostly with low numbers of species in Florida rivers.

These three factors can be combined in a single empirical model describing the numbers of unionid species in rivers of our biogeographic system:

$$S = CA^z (a_1 X^{AC} + a_2 X^{SV}) + b_1 (H) + b_2 (DS) + b_3 (NO_3) + k + \epsilon \quad (5)$$

where,

S = number of species,

A = area of drainage basin,

AC, SV = stepping-stone distances from the Alabama-Coosa and Savannah Rivers, respectively,

H, DS, NO_3 = hydronium concentration, dissolved solids, and nitrate concentrations, respectively,

k, C, z, X, a_1 , b_1 = statistical parameters to be estimated,

ϵ = residual error.

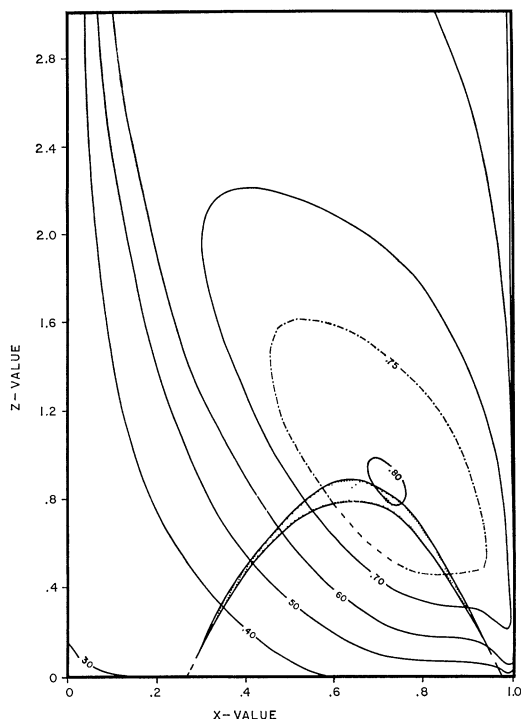


FIG. 9.—Isopleth plot of the coefficient of multiple determination (R^2) for text Equation 5 for various values of z (vertical axis) and X (horizontal axis). The maximum R^2 is 0.8022 occurring at $z = 0.87$ and $X = 0.72$. A one-sided lower confidence limit at the 0.05 level for the maximum R^2 is approximately 0.70. The stippled parabola covers the points for which the ratios of a_1 to a_2 are in the range 2.4 to 2.9, which is the ratio of number of species in the Alabama-Coosa River System (50 to 60) to number in the Savannah (21).

The best fit of this equation, calculated by multiple regression with iterations of z and X , accounts for slightly more than 80 percent of the variance in numbers of species. The biogeographic variables (A, AC, SV) are by far the most important, together explaining 64.5 percent of the variance; $A^z X^{AC}$ alone encompasses almost 45 percent. Dispersal distances from the two other postulated source rivers, the Apalachicola and St. Lawrence Rivers, are insignificant, together adding less than 0.001 to the coefficient of multiple determination (R^2). The linear environmental quality variables account for

5.4, 5.7, and 4.6 percent of the variance, respectively as listed above.

The values of z and X producing the best fit are 0.87 and 0.72. However, these parameters have very wide confidence intervals with both able to vary over large ranges while changing R^2 only slightly. This is indicated in Figure 9, an isopleth graph of the coefficient of multiple determination versus z and X . Much of the possible variation is due to two causes:

1. Drainage basin area is only a rough estimate of wetted area within a river system; stepping-stone distance treats rivers as separated by integral distances, whereas true dispersal distance varies between every pair of rivers.

2. Values of z and X are, in fact, rather insensitive to true biogeographical variations; in our simulations of stepping-stone processes we found that small changes in immigration and extinction probabilities greatly altered the base of the geometric series in species numbers. Thus, from an empirical standpoint, knowing X allows only rough estimates of these probabilities.

However, even with a large amount of statistically insignificant variation in the estimates of the parameters, we can perform an independent test of the model to assess its accuracy. In the discussion of immigration by stepping stones, we showed that the parameter a_1 ($= P_1/k$) in the geometric series describing the decline in diversities away from a source should be proportional to the size of the species pool in the source. Thus, in our empirical model, the ratio a_1/a_2 should equal the ratio of the number of species in the Alabama-Coosa River to that of the Savannah. The Alabama-Coosa has 50 to 60 species of freshwater mussels and the Savannah has 21, a ratio of (2.4–2.9):1. The shaded parabolic area in Figure 9 covers the points for which solutions of the model satisfy this criterion. Although the parabolic area does not coincide exactly with the maximum R^2 ($a_1/a_2 = 2.96$), it falls gratifyingly close.

Still, there remains a problem with the

constant k in the model (5). For the maximum fit, the value of k is approximately 10.1, very close to the average number of species (11.5) in the analyzed rivers. This would indicate that the variables are merely correcting the average number of species for the peculiarities of each river and that a river with a negligible drainage basin very distant from any source river could still support about 10 species, an intuitively unappealing consequence. However, at other values of z and X , these problems are reduced. The solution of the model at $z = 0.30$ and $X = 0.90$ has a k -value of 3.3, which reduces to nearly 0 when corrected for the average values of the linear environmental quality variables. This solution also yields several other interesting results. First, these values of z and X are close to the z -value (0.316) and average X -value (0.938) calculated in the independent analyses of area and distance effects above. Second, z and X are on the left-limb of the parabola in Figure 9, so the coefficients a_1 and a_2 are within the correct range of proportions. In this solution, distance from the St. Lawrence River (A^2X^{SL}) becomes a marginally significant variable ($\Delta R^2 = +0.035$). The St. Lawrence has 26 species, a ratio of 1.24 with the species pool of the Savannah River. In the solution of the model, the ratio a_3/a_2 is 1.31, very close to the predicted value. This, in combination with the other characteristics of this solution, indicates it is a more realistic model of species numbers in the biogeographic system. And, although the coefficient of multiple determination (0.733 including the St. Lawrence) is less than the maximum (0.802), it is well within the 0.95 confidence interval of the maximum R^2 .

DISCUSSION

The empirical model we have proposed for describing unionid species numbers in coastal rivers of the eastern United States is based on an interactive effect of area and isolation on species numbers. Although we have no *a priori* basis for the exact algebraic form of the interaction, our model

does meet many of the requirements of MacArthur and Wilson's (1967) theory of island biogeography. The model states that the effect of area on numbers of species (dS/dA) decreases as stepping-stone distance from the source areas increases. Also, it meets the boundary conditions that islands of very small areas or of great distance from species sources will have few if any species. Diamond (1972, 1973) independently derived a similar algebraic description of species numbers for birds on islands in the southwest Pacific Ocean.

The variables describing environmental quality in our model should not strictly be linear, but rather interactive with area, diminishing the parameter C with increasing environmental harshness. However, because of the subordinate role of these variables and the complexities of solving such an algebraic model with our methods, we consider a linear solution to be adequate.

Although our model stresses the importance of distance effects, the relative importance of the various source rivers is not entirely clear. Stepping-stone distance from the Apalachicola River is not an important variable in the solution of the model since it is highly redundant ($r > 0.90$) with distance from the Alabama-Coosa, which has a slightly higher correlation with species numbers. The large number of species (33) in the Apalachicola is due in part to its proximity to the Alabama-Coosa.

Reasons for the low significance of distance from the St. Lawrence River are less obvious. Johnson (1971) suggested that the rivers of the Northern Atlantic slope were mostly recolonized after Pleistocene glaciation from the south rather than from the north. Since the St. Lawrence has a smaller species pool than the south as a whole, we should not expect it to be as influential on the distribution of species. More importantly, because of its long tidal estuary, the St. Lawrence may actually be further removed from the biogeographic system than our method of counting stepping-stones indicates.

Temperature effects may also serve to diminish the influence of the St. Lawrence River. In our multiple regression analyses (Appendix II), temperature variables had an uninterpretable relationship with species numbers when regressed with dispersal distances, because of statistical redundancy. Thus, temperature is absent from our final model. This does not mean that numbers of species is unrelated to temperature. Very probably, high variation in temperature in the north reduces the probability of successful colonization of new rivers by increasing mortality among invading propagules. Low winter temperatures which result in ice on the rivers clearly reduce the portion of the year during which immigration can occur. Both of these factors effectively increase isolation from the St. Lawrence. Furthermore, the small number of species in the St. Lawrence relative to its size may be a consequence of variable temperatures.

Another factor responsible for low numbers of species in the northern rivers may be recency of colonization. Wilson (1969) postulated that several kinds of species equilibria are possible depending on the duration of time over which colonization has occurred. The first equilibrium reached on a newly habitable island is termed "non-interactive" and is characterized by relatively low population densities. As the number of individuals approaches the island's carrying capacity, some species become extinct as a result of biological interactions; the resulting equilibrium is therefore termed "interactive." Subsequent turnover in species composition leads to a higher "assortative" equilibrial assemblage which is more ecologically suited to the particular physical and biological environment presented by the island. Finally, over a longer period of time, genetic adaptation may result in lowered rates of extinction and a higher "evolutionary" equilibrium.

The northern portion of the coastal biogeographic system was almost entirely glaciated during the Pleistocene. Thus, the St. Lawrence and other northern rivers

have been available to colonization for a period on the order of only 10,000 years. This group of rivers may therefore harbor a group of species in assortative equilibrium. Rivers to the south remained unglaciated and subsequently have had more time to approach evolutionary equilibria. The greater number of endemic species in the southern rivers (see Fig. 2) supports this contention. We wish to stress the distinction between the mechanisms just proposed and the notion in classical unionid zoogeography that northern rivers are depauperate because few species have been able to reach them at all during the short period of time since the Pleistocene.

The high statistical significance accorded in our analysis to distance from the Savannah River is also problematical, since this river was somewhat arbitrarily chosen as a possible species source. To test the uniqueness of the Savannah as a source, we replaced it in equation 5 with distance from the Cooper-Santee River System. The Cooper-Santee has as many species (21) as the nearby Savannah and appears to have also had geomorphic confluence with the Interior. The best solution of the model with the Cooper-Santee has a coefficient of multiple correlation nearly identical to that with the Savannah. Thus, we infer that no single river within the Southern Atlantic Slope province is the primary species source, but that this province as a whole is acting as a source for neighboring regions. In our simulations of species numbers along stepping-stone islands, we observed that if an island or cluster of islands well removed from the primary source were given maximum diversities, these islands would retain high numbers of species for relatively long periods of time. Each island within the cluster would reinforce the others by contributing species that became extinct locally. Furthermore, the rest of the system would equilibrate to the species-rich cluster and display a geometric decline in species numbers away from it. Thus, a quasi-equilibrium would be maintained and only

after a long duration would true equilibrium with the primary source be re-established. Such a quasi-equilibrium is probably operative in the Southern Atlantic province, which has gained more than its expected complement of species through Holocene stream capture with rivers of the Gulf and Interior regions.

Processes of immigration

Our analysis has been based upon the assumption that species numbers in the coastal river systems are in an equilibrium, produced by a balance of continual immigration and extinction. The success of the analysis suggests that these assumptions are justified. Evidence of local extinctions has already been presented by the observation of certain disjunct species ranges. It can be postulated from this that any species in a river system has a positive, if small, probability of extinction during some given span of time. Therefore, if a local fauna is considered as a whole, there must be an expected rate of extinction.

In order to justify our assumption of relatively frequent immigration it is necessary to demonstrate that dispersal of unionids need not be solely dependent upon episodic stream capture and coastal flooding. However, at present, specific processes of inter-river immigration are a matter of speculation. We would like to suggest several possible mechanisms. The first is to revive the idea that birds are agents of dispersal. An old hypothesis, reviewed and rejected by van der Schalie (1945), proposes that gravid mussels occasionally attach to the feet of aquatic birds and are then transported into neighboring river systems. Another possibility he did not consider is that predatory birds might carry parasitized fish or parts of fish (especially gill filaments) across divides and into adjacent rivers. Such an event could introduce hundreds of glochida into a foreign river system, giving the species a strong chance for successful colonization.

A more important means of immigration

may be secondary and peripheral fishes. These behave like true freshwater fishes but are not absolutely confined to freshwater, being able to withstand extended periods (days, weeks, or even months) at sea (Myers, 1937). Glochidia might be transported along the coast between river systems while encysted in the gills or body surface of secondary and peripheral fishes. Of 33 species of fish found to carry glochidia by Howard (1912), Surber (1912), Coker et al. (1921), and Johnson (1946), ten (30%) were secondary or peripheral. And, of the 27 species of unionids examined by these authors, 18 (67%) employed a secondary or peripheral fish as one of its hosts. This sample is admittedly small and only two species found to parasitize secondary or peripheral fishes (*Anodonta implicata* and *Lampsilis anodontoides*) are members of the eastern coastal fauna. Still, it does suggest that these fishes serve to disperse unionids between river systems. A sea journey, induced by storms, spring floods, migrations of peripheral fishes, etc., need not be a long one; any of the numerous small coastal streams between the large river systems considered in this study could act as temporary staging grounds, lasting perhaps tens of generations, before passage to other rivers occur.

These possible means of dispersal by birds and fishes are presumably very low probability events. However, given enough time, they might sum up to the slow rates of immigration necessary to counterbalance extinction and produce the observed equilibrium numbers of species in the river systems.

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APPENDIX I

Data

Species numbers of freshwater mussels in 32 coastal rivers in southeastern United States were compiled from the faunal lists of Johnson (1970, 1972); Johnson also kindly made available faunal lists for 17 additional rivers north of the Potomac. Complete sets of physical data for 44 of the rivers are analyzed below. These rivers are inhabited by 79 species with the number of species in any single river ranging from 2 to 33; the mean number of species is 11.5 with a variance of 36.63.

Several time-independent parameters that may be influencing this variance in species numbers include area of habitat islands, dispersal distances, diversity of habitats, and general environmental quality. A number of relevant measures of these parameters were compiled from several sources and are summarized below.

Area of drainage basins (A). The time that would be involved in measuring the wetted area of a single large river system could make insular biogeographic modeling impossible. However, several regularities in the development of drainage systems suggest a method for deriving suitable estimates of habitable area. Schumm (1956) has demonstrated that the total length of waters within a river system is linearly proportional to the area of its drainage basin (see also Strahler, 1957). Width of a river displays an exponential relationship to total upstream length (M. Woldenberg, pers. comm.). Therefore, total wetted area, and thus potentially habitable area, is a nonlinear function of the total drainage area.

We measured drainage areas using a polar planimeter from the Water-Supply Maps of the United

States Geological Survey. Measurement of each basin was made along the perimeter defined by the drainage divides and the coast; area of the tidal estuary was subtracted from the total area.

Dispersal distance. The relative isolation of rivers cannot be measured by various permutations of "shore-to-shore" distances as it has in other statistical analyses of insular biogeography. Linear distances between rivers are considered invalid since it is not immediately obvious what part of a river system should be used as an end point. It is also unclear whether distance should be measured on a straight line, along the irregular coasts, or by some other means. An alternative measure of dispersal distance, and the one chosen here, is suggested by the generally linear arrangement of the rivers along the coast. Each river can be considered a stepping stone, and dispersal distance can be estimated as simply the number of steps from a species-source river. This measure is certainly no better than linear distances, but its simplicity is appealing. Furthermore, this measure can be readily manipulated in theoretical considerations. In counting stepping stones, rivers that share a common small estuary were considered single stepping stones. The rivers of peninsular Florida south of the Waccasassa and St. Marys exclusively are all interconnected by more or less continuous freshwater swamp; these rivers were therefore all given the same stepping-stone distances.

The designation of certain rivers as probable species-source areas from which to count stepping-stone distance was influenced by several criteria: (1) the river must be within or close to the boundaries of the biogeographic system; (2) it must display a relatively high number of unionid species; (3) it must contain a number of species whose ranges include neighboring river systems; and (4) the river must be of apparent historical importance, being a route by which species could have dispersed directly from one faunal province to another. Four rivers fit these criteria best:

Alabama-Coosa River System (AC). This large river system bounds the eastern Gulf slope faunal province to the west. It contains 50 to 60 species, probably representing more than half of the total fauna of the Interior Basin (R. I. Johnson, pers. comm.). This large number of species is probably due largely to its proximity to the Mississippi. However, some of its species were derived from the Tennessee River System during the Holocene stream capture. Subsequent stream capture between the Alabama-Coosa and Apalachicola and Escambia Rivers permitted a number of species to enter the Gulf province (Johnson, 1970).

Apalachicola River (AP). This is the most diverse river among those directly under consideration. Its Holocene confluence with the Alabama-Coosa probably augmented this large number of species. Many of the Apalachicola's 33 species are widely distributed throughout the Gulf, Florida,

and Southern Atlantic biogeographic provinces (Fig. 2). Transfer of species was aided by geomorphic confluence between the Apalachicola and Savannah Rivers (Johnson, 1970).

St. Lawrence River (SL). This large river to the north of the biogeographic system shares 11 of its 26 unionid species with rivers in the relatively depauperate Northern and Middle Atlantic Slope provinces (Johnson, pers. comm.). The St. Lawrence and its ancestral drainages had contact with the Interior Basin during the Quaternary and may have acted as dispersal routes around the northern end of the Appalachian Mountains (Johnson, 1970).

Savannah River (SV). The Southern Atlantic Slope province is inhabited by a number of species that do not occur in any of the source rivers discussed above. These unionids are endemics, relicts, and species of Interior origin that have reached the Southern Atlantic Slope by various routes. The rivers of this province are relatively rich in species and have affected the faunal composition of the neighboring Florida and Middle Atlantic Slope provinces. Early statistical analysis (see Appendix II) demonstrated that the number of species in the Southern Atlantic province could not be explained with the three source rivers discussed above. However, choosing one river as a species source from this province is somewhat arbitrary. The Savannah River is relatively rich (21 species) for its size and apparently has been a dispersal route for species from the Gulf region during confluence with the Apalachicola. Therefore, the Savannah is probably the best choice as an operational source. However, it should be noted that the Altamaha, Cooper-Santee, and Cape Fear Rivers, among others, might also have been chosen.

Other rivers, including the Roanoke, James, Hudson, and Susquehanna, have received several species from the Interior Basin during stream capture with rivers west of the Appalachian Divide (Johnson, 1970). However, these have little influenced the faunal composition of the coastal biogeographic system as a whole and were not considered in our analyses.

Environmental quality variables. Green (1971) and Cvancara (1970) have reviewed the influence of several environmental parameters on the distribution of freshwater mussels. From these we selected variables that were thought to be relevant either to the regulation of species numbers or specifically to the physiological tolerances of unionids. Data for several of these variables were found in the Water Supply Papers of the United States Geological Survey. Only freshwater stations closest to the mouths of the rivers were used to obtain data. Since the discharge of a stream is proportional to its length (Leopold, Wolman, and Miller, 1969), a river may be viewed as a vast mixing system with the characteristics of the water at any one point being an average of characteristics upstream. Thus,

a measurement at the mouth represents the entire system better than any other *single* measurement along the course of the river. Each datum in this study is a mean of from 1 to 40 measurements (generally 5 to 10) taken whenever possible from records for 1968. We did not feel that the data in the Water Supply Papers could be used to estimate comparable variances in environmental quality for the rivers; the number of gaging stations with available data varies among rivers and stations are irregularly spaced along each river. The following environmental variables were used in the analysis.

Mean annual temperature (TM) and *annual temperature variance* (TV). These two variables correlate highly with the tropical to polar diversity gradients observed among numerous groups of organisms (Pianka, 1966). Sanders (1968, 1969) inferred a causal relationship between temperature variance (reflecting environmental predictability) and numbers of species.

Chloride concentration (Cl). Cvancara (1970) has demonstrated chlorinity to be an important factor limiting the distribution of freshwater mussels.

Nitrate concentration (NO₃). Nitrate is a final oxidation product of organic material and is an important factor for the growth of algae and bacteria (Hutchinson, 1967), which are probably major food sources for unionids.

pH. This is an important factor in shell calcification (Wilbur, 1967) and low pH is thought to severely restrict the distribution of many unionids (Johnson, 1970). In most of our analyses we used *hydronium concentration* (H), which is simply the base-ten antilog of the negative of pH.

Calcium concentration (Ca), *bicarbonate concentration* (HCO₃), and *carbonate hardness* (H-C). These variables reflect the availability of dissolved calcium carbonate, which plays a major role in the formation of unionid shells (Wilbur, 1967).

Noncarbonate hardness (H-N). This is the water hardness caused by carbonate and bicarbonate concentrations in excess of the equivalent of calcium and magnesium ions. Presumably, it reflects the presence of other metals in the water, some of which may be detrimental to unionids.

Dissolved solids (DS). This variable is the amount of solid residue left after evaporation of the water at 180° C for one hour. It reflects the total amount of mineral matter in solution and suspension and correlates with both carbonate concentration and salinity. Thus, the influence of dissolved solids on freshwater mussels is somewhat ambiguous.

Below are the data used in the final multiple regressions.

Nitrate concentration (NO₃) and amount of dissolved solids (solid residue) are in parts per million; hydronium concentration (H⁺) is in gram-ions times 10⁷.

River	Number of Species	Area (mi. ²)	No. of Stepping Stones				NO ₃	Solid residue	H+
			AC	AP	SV	SL			
Penobscot	9	8440	33	28	21	4	0.80	57	4.00
Kennebec	8	5960	32	27	20	5	0.40	31	3.20
Androscoggin	7	3510	31	26	19	6	0.60	65	2.50
Saco	6	1730	30	25	18	7	0.80	33	2.50
Merrimac	11	5020	29	24	17	8	2.60	78	6.30
Blackstone	8	425	26	21	14	11	8.40	120	20.00
Thames	7	1480	25	20	13	12	3.50	86	3.20
Connecticut	11	11500	24	19	12	13	1.30	75	2.50
Housatonic	11	2050	23	18	11	14	2.10	138	1.00
Hudson	14	13500	22	17	10	15	0.80	101	0.63
Delaware	13	11100	21	16	9	16	8.70	122	3.20
Susquehanna	11	27900	24	21	12	21	3.40	164	1.30
Potomac	14	14400	23	20	11	20	3.70	156	0.50
Rappahannock	9	2560	22	19	10	19	1.10	47	2.00
York	7	2790	21	18	9	18	0.70	59	2.00
James	12	9850	20	17	8	17	1.20	102	1.60
Chowan	9	4870	19	16	7	18	1.20	99	1.60
Roanoke	10	9680	19	16	7	18	4.10	85	1.30
Pamlico	12	4150	18	15	6	19	1.80	82	1.00
Neuse	15	5490	17	14	5	20	2.60	76	1.60
Cape Fear	20	9000	16	13	4	21	1.30	78	2.00
Waccamaw	10	2100	15	12	3	22	0.70	30	10.00
Pee Dee	13	14400	15	12	3	22	0.50	57	3.20
Cooper-Santee	21	17300	16	11	2	23	0.50	57	3.20
Edisto	8	3440	13	10	1	24	0.80	53	1.60
Savannah	21	10800	12	9	0	25	0.60	49	5.00
Ogeechee	12	4360	11	8	1	26	0.10	55	1.60
Altamaha	18	14700	10	7	2	27	0.60	45	1.00
Satilla	2	3720	9	6	3	28	0.20	29	32.00
St. Marys	4	1870	8	5	4	29	0.50	64	20.00
St. Johns, Fla.	10	8800	7	4	5	30	0.90	391	1.00
Kissimmee	7	3190	7	4	5	30	0.90	88	1.30
Peace	9	2260	7	4	5	30	0.80	257	0.50
Myakka	6	657	7	4	5	30	0.20	105	1.60
Alafia	3	521	7	4	5	30	1.60	520	3.20
Hillsborough	8	719	7	4	5	30	0.60	171	0.40
Withlacoochee	9	2120	7	4	5	30	0.30	229	0.20
Waccasassa	2	349	6	3	6	31	1.00	461	0.25
Suwannee	13	10100	5	2	7	32	1.00	133	0.40
Ochlockonee	20	3010	4	1	8	33	0.80	81	1.60
Apalachicola	33	19700	3	0	9	34	0.70	55	1.60
Choctawhatchee	18	4770	2	1	10	35	1.10	57	1.00
Yellow	11	1380	1	2	11	36	0.20	44	3.20
Escambia	23	4270	1	2	11	36	0.10	61	2.00

APPENDIX II

Multiple regression analysis

The table below is an abbreviated history of the development of text equation 5. It summarizes various stepwise multiple regressions assessing the contributions made by several biogeographic and environmental variables to the variance in unionid species numbers within our biogeographic system. Symbols for the variables are explained in Appendix I. The number in each block indicates the increase in the coefficient of multiple determination (R^2) caused by the addition of that variable into

the regression; information is given only for variables up to and including the last entered with a contribution to R^2 greater than 0.01. The sign of the regression coefficient is given in the upper lefthand corner. Significance levels are indicated by asteriks in the upper righthand corner, where $P < .01$ is denoted by ** and $P < .05$ by *. Blocks with crosses indicate variables that were not used as independent variables. "lin." denotes linear multiple regressions, and "log." denotes regressions in which all variables, including species number, were transformed to logarithms. Species number is the independent variable in all cases.

		Biogeographic						Environmental										total R ²
		A	AC	AP	SV	SL	I	TM	TV	H	DS	NO ₃	Cl	Ca	HCO ₃	H-C	H-N	
1	lin.							.0430		.1425	.1082	.0156						.3093
	log.										.0241	.0613	.0395	.0739	.0915	.0214	.1533	.4651
2	lin.	.3048							.0607	.0495		.0102				.0311	.0737	.5301
	log.	.4170										.0210		.0579		.0499	.0677	.6136
3	lin.	.3048							.0731	.0722	.0640	.0149						.5290
	log.	.4170							.0154	.0239	.0420	.0078						.5062
4	lin.	.3048					.0688	.0359		.0716	.0764	.0199						.5770
	log.	.4170					.0445	.0129		.0206	.0277	.0345						.5574
5	lin.	.3048	.1084			.0482		.1393		.0510	.0493	.0251						.7265
6	lin.	.3048	.1084			.0344				.0718	.1217	.0246						.6658
7	lin.	.3048	.0105	.2423	.0332					.0529	.0890	.0248						.7576
8	lin.	—	.6154		.0763					.0565	.0359	.0157						.7992

1. All the environmental quality variables, no biogeographic variables. In the logarithmic regression, the signs of *Cl* and *H-C* are unexpected and represent uninterpretable and probably spurious relationships, resulting from the high correlation between these two variables.
2. Area and all environmental variables. In the logarithmic regression, opposite signs on the estimated parameters of two highly intercorrelated measures of water hardness, *Ca* and *H-C*, are uninterpretable statistical artifacts. The estimate of *z* (the parameter for *A* in the logarithmic multiple regressions) is 0.284, ranging from 0.302 to 0.348 in steps 1 to 4.
3. Models similar to 2 except that the measures of environmental quality have been reduced to five, eliminating problems of uninterpretable signs. Note that in both the linear and logarithmic regressions, area alone accounts for more than half of the explained variance in species number. The estimate of *z* in the logarithmic regression is 0.306, ranging from 0.283 to 0.348 in steps 1 to 4.
4. Models similar to 3 except that a measure of isolation has been added. *I* is the number of stepping stones (rivers) from the nearest species-source river (either the Alabama-Coosa or the St. Lawrence). This is similar to a measure used by Brown (1971) in his analysis of boreal mammals in the Great Basin. The estimate of *z* in our logarithmic regression is 0.312, ranging from 0.313 to 0.378 in steps 1 to 5. At this point in our analyses, the logarithmic models began to explain consistently less variance in numbers of species than did linear versions and therefore are not considered further.
5. Model similar to the linear model in 4 except that *I* has been replaced by numbers of stepping stones from both the Alabama-Coosa and the St. Lawrence. *I*, the distance from the nearest species source, assumes that both source rivers have equally-sized species pools and that there is equal ease of immigration in both directions. The first assumption is certainly invalid since the St. Lawrence holds 27 species whereas the Alabama-Coosa holds 50 to 60. A more realistic way to measure dispersal distances is to consider as separate variables the number of stepping stones from each source. The difference in relative influence of species pools in the Alabama-Coosa and St. Lawrence is evinced in the difference between the regression coefficients of these two variables, -1.484 and -0.865, respectively. Note that the sign of the regression coefficient for mean annual temperature (*TM*) is negative; this relationship is probably spurious, resulting from high correlations with measures of dispersal distance.
6. Model similar to 5 except that both temperature variables have been eliminated. This regression displayed large positive residuals for rivers of the Southern Atlantic and Gulf Slope regions and led to the inclusion of dispersal distances from the Savannah and Apalachicola Rivers in subsequent regressions.
7. Model with area, four dispersal distances, and three environmental variables. The dispersal distances used in this regression are *reciprocals* of the numbers of stepping stones from the various source rivers, reflecting the inverse relationship between species numbers and degree of isolation (Wilson, 1969). Power (1971) used an inverse measure of dispersal in his analysis of numbers of bird species on California islands.
8. Interactive model with the dispersal distances expressed as *A/AC*, *A/AP*, *A/SV*, and *A/SL*. The reversal in importance of *AC* and *AP* in models 7 and 8 reflects the high correlation between these two variables.